here or with *P. lanceolata*. The description of the leaf applies to either, and neither Muhlenberg nor Elliott mentions the diagnostic characters. It is probable that *Unisema heterophylla* Raf. Med. Fl. ii. 108 (1830), "From New York to Louisiana" was based upon both this and the next.

P. LANCEOLATA Nutt. Gen. i. 216 (1818). *P. cordata*, var. *lanceolata* (Nutt.) Griseb. Cat. Pl. Cub. 252 (1866).—South Carolina to Texas and Paraguay. Since this species has been confused with *P. cordata*, forma *angustifolia*, it is desirable to cite characteristic specimens. GEORGIA: between Weycross and Ruskin, Ware Co., *Harper*, no. 1469. FLORIDA: Indian River, *Palmer*, no. 538; Duval Co., *Curtiss*, no. 2988,* *Fredholm*, no. 5126; South Jacksonville, April 7, 1897, *Churchill;* Eustis, Lake Co., *Nash*, no. 450. TEXAS: *Lindheimer*, no. 194. CUBA: "introduced" in river, Taco Taco, Pinar del Rio, *Wright*, no. 3260; Coloma, Pinar del Rio, *Britton & Cowell*, no. 9693. BRAZIL: Matto Grosso, *Leeson*. PARAGUAY: in regione cursus superioris fluminis Apa, *Hassler*, no. 7849.

Forma **trullifolia**, n. f., forma typica recedit foliis anguste deltoideo-ovatis basi truncatis vel subcordatis.—VIRGINIA: Point Micon Reach, *Tidestrom*, no. 82. NORTH CAROLINA: Spencer, July 12, 1919. *P. O. Schallert.* FLORIDA: Okeechobee region, Brevard Co., August 3, 1903, *Fredholm*, no. 5927 (TYPE in Gray Herb.); Eustis, Lake Co., *Nash*, no. 449. TEXAS: San Patrico, *Lindheimer*, no. 2516; Houston, *Lindheimer*.

Forma **brasiliensis** (Solms), n. comb. *Urisema acutifolia* Raf. Med. Fl. ii. 107 (1830) based upon the characteristic figure in Lam. Encyc. t. 225 (1793). *P. cordata*, forma *brasiliensis* Solms in DC. Monogr. iv. 533 (1883).—The following are characteristic. FLORIDA: without definite locality, *Chapman* (Bilt. Herb. no. 752*c*); Duval Co., *Fredholm*, no. 5237; Port Orange, *Straub*, no. 134; Fort Myers, *Hitchcock*, no. 354, *J. P. Standley*, no. 104. LOUISIANA: Gretna, *Ball*, no. 329. PARAGUAY: central Paraguay, *Morong*, no. 490; near Lake Ypacuray, *Hassler*, no. 12,683; Sierra de Maracayú, Hassler, no. 5363.

GRAY HERBARIUM.

POSSIBILITIES OF HYBRIDISM AS A CAUSE OF VARIATION IN POLYGONUM.

E. E. STANFORD.

DURING the last century a considerable number of hybrids within the subgenus *Persicaria* of the genus *Polygonum* have been reported in Europe. On the American side very little attention seems to have

been paid to the possibility of such crosses. From a comparison of Focke,[1] Figert,[2] Ascherson & Graebner,[3] and other sources, it appears that the first *Persicaria* hybrids to be announced as such were published as *Polygonum minori-Persicaria* and *P. dubio-Persicaria* by Alexander Braun[4] in 1824. What Ascherson & Graebner regard as the same plants have subsequently been frequently reported under various designations, and are now referred by them to *Polygonum Persicaria* × *minus* and *P. Persicaria* × *mite* (*P. dubium* having been reduced to *P. mite* Schrank). Since this early publication a considerable number of other *Persicaria* hybrids have been listed by various writers; the Ascherson & Graebner treatment, for example, enumerating the supposed results of such crossings under all the European species listed by them with the exception of *Polygonum amphibium* L. which appears, from examination of the literature, not to be considered to hybridize. This is not surprising, for *P. amphibium*, though extremely variable, is considered to have no close relatives in Europe, all the forms and varieties occurring there being generally considered to be below specific rank.

The criteria upon which reliance has been placed in the detection of hybrids have usually been demonstrable blending of the characters of the supposed parents, the presence of the latter in the vicinity, a greater or less degree of sterility, and often vigorous growth coupled with the production of unusually conspicuous flowers. The European Persicarias, with the exception of *Polygonum amphibium*, are annuals, and the hybrids, on account of their usual considerable sterility, have not usually been considered as becoming independently established or self-maintaining. The majority of these proposed hybrids, according to their bibliographies as given in the Ascherson & Graebner treatment, have mostly also been published by other authors as varieties or new species. The annual Persicarias, as shown in a previous paper[5], are usually extremely productive of normal achenes, and the character of sterility has therefore been especially accentuated by most students who have described otherwise puzzling or "off-type" specimens as hybrids.

[1] Focke, Die Pflanzen-Mischlinge, 348, 349 (1881).

[2] Figert, *Ueber Bastarde aus der Gattung Polygonum.* Allgem. Bot. Zeitschr. i. 26–30 (1895).

[3] Aschers. & Graebn. Syn. Mitteleur. Fl. iv. 800–875 (1913).

[4] A. Br. Fl. vii. 359, 360 (1824).

[5] Stanford, Rhodora, xxvii. 41-47 (1925).

Hy,[1] one of the few European authors to have published on floral dimorphism in *Persicaria*, was interested also in hybridism, and summed up his observations in part as follows:

"1. Dans les espèces annuelles de la section Persicaria les fleurs présentent un cas remarquable de dimorphisme par cleistogamie: sur la même inflorescence, les ûnes restent closes et fertiles, les autres s'ouvrent mais demeurent d'ordinaire stériles, faut de pouvoir se féconder elles-mêmes.

2. Dans les plantes normales les fleurs ouvertes et stériles sont toujours en moindre nombre même sur les espèces qui en présentent le plus comme P. Persicaria L. et P. mite Schr.

3. Dans quelques individus disseminés en petit nombre au milieu de lêurs congénères, ces mêmes fleurs ouvertes et stériles existent seules ou à peu près, d'où il result stérilité complète ou presque complète pour la plante entière . . . dans . . . P. Persicaria × P. mite la proportion des fleurs fertiles était seulement de 1/150; dans . . . P. Persicaria × P. minus, 3 graines seulement se sont rencontrées sur 10 pieds . . . P. minus × P. hydropiper, n'a présenté aucune graine fertile. Ma conclusion était celle-ci: l'hybridité seule a pu causer cette stérilité."

Hy was also familiar with the type of heterostyly displayed by *Polygonum amphibium* L., which he considered of a type "absolument distinct . . . un example de plus à ceux . . . plantes physiologiquement dioques . . . sur les ûnes les styles sont courts, les étamines longuement saillantes et les fleurs demeurent stériles; sur les autres, les fleurs n'ont de saillant que le style mais produisent de beaux et bons fruits."

Of more recent writers Schuster[2] in his revision of *Polygonum lapathifolium* L. devoted considerable attention to hybridism as concerning his conception of this species and the numerous subdivisions which he made of it. He noted the occurrence of sterile pollen both in hybrids and in what he considered pure species, and stated:

"Allein der s t e r i l e P o l l e n bietet überhaupt kein sicheres Merkmal zur Erkennung von Polygonum-Bastarden, weil auch die Ähren der reinen Arten einen mehr oder weniger schlechten Pollen besitzen und unfruchtbar sind. Von den Polygonum-Bastarden wird in der Literatur allgemein behauptet, dass sie unfruchtbar sind; ich konnte indessen nicht e i n e n Bastard finden, der vollkommen unfruchtbar gewesen wäre; allerdings ist die Fruchtbarkeit eine r e d u z i e r t e indem in der Regel die Ähren eines Bastards mehr unfrucht-

[1] Hy, Troisième Note sur l'herborisation de la Faculté des Sciences d'Angers (1882); *Sur le dimorphisme floral dans quelques especes du genre "Polygonum."* Rev. de Bot. iv. 87–89 (1885).

[2] Schuster, *Versuch einer natürlichen Systematik des Polygonum lapathifolium* L. Mitteil. Bayerisch. Bot. Gesellsch. ii. 50–59 and 74–78 (1907).

bare Blüten zu enthalten pflegen als die reinen Arten . . . Samen von P. mite × Persicaria . . . die ich aussäte, keimten rasch und leicht. Natürlich können auch vollständig sterile Hybriden bei Polygonum vorkommen, jedenfalls aber ist dies nicht die Regel. . . ."

Schuster also noted that poorly nourished plants of *Polygonum Persicaria*, for instance, produced few fruits and by some botanists had therefore been taken for hybrids. He found pollen characters to be rather variable, and that hybrids often attracted attention by their unusual vigor. As to the pollen, further:

"Die sterilen Pollen, von denen ganz wie bei den reinen Arten bald ein grösserer bald ein geringerer Prozentsatz vorhanden ist, sind im allgemeinen nur halb so gross als die fertilen; bei P. mite × Persicaria mes en leitztere im Mittel 0,042 mm, die sterilen 0,021 mm."

He found variations in the pollen relief-markings of some hybrids which he believed to result from a blending of parental characters. He came to the conclusion that:

"P. lapathifolium nicht nur s t a r k v a r i i e r t, sondern auch s e h r l e i c h t b a s t a r d i e r t;" and enumerated 7 "Wirkliche Bastarde" and 3 "Vermeintliche Bastarde."

"Es ist im höchsten Grade w e h r s c h e i n l i c h, dass die sog. n i c h t h y b r i d e n Ü b e r g a n g s f o r m e n der systematisch einander nahestehenden Polygonum-Arten nur F o r m e n p o l y m o r p h e r H y b r i d e n sind, die auch als h y b r i d o g e n e Arten auftreten können; wenigstens ist dies bei P. m i t e v a r a m b i g u u m T h e l l u n g und P. f o l i o s u m L i n d b. fil. der Fall."

These he had previously noted as forms of "dem polymorphen Bastard P. Hydropiper × mite." One emerges from the discussion with the feeling that what is really needed is the experimental production of a few hybrids in this subgenus, under controlled conditions, and a subsequent study of their behavior and characters. Owing perhaps to the small economic importance of these plants, and perhaps also to the inconveniently small size of the flowers, nothing of this sort appears to have been attempted.

Apparently the only American hybrid *Persicaria* thus far described as such in the American literature—at least in recent time—is *Polygonum hydropiperoides* × *robustius* Fernald.[1] Because of the bearing of this plant on the following discussion the original publication is quoted in full:

"P. hydropiperoides × robustius, n. hybr., caule decumbente basi valde lignescenti stoloniferoque plerumque 3–5 mm. crasso;

[1] Fernald, RHODORA, xxiv. 173, 174 (1922).

ramis floriferis adscendentibus 0.3–1 m. longis; foliis anguste ellipticis vel elliptico-lanceolatis acuminatis vel acutis 0.5–2 dm. longis 0.8–4 cm. latis; ocreis laxe cylindricis strigosis ciliatis, ciliis 2–5 mm. longis; pedunculis erectis elongatis; spicis filiformibus plerumque 0.4–1 dm. longis alternifloris, rhachi purpurascenti; ocreolis ciliatis: perianthiis lacteis 2–3 mm. longis, epunctatis vel rare punctatis: achaeniis vacuis.

Nova Scotia: in great abundance in peat and granite gravel bordering outlet of Lamb's Lake, Annapalis Co., July 19, 1921 (foliage), *Fernald, Bartram, Long & Fassett*, no. 23,802, August 29, *Fernald & Long*, no. 23,803 (type in Gray Herb.) and in *Pl. Exsicc. Gray.* September 16, *Donald McPherson*, no. 23,804.

Exactly combining the aspect and characters of the two species, both of which occur with or near it. In its coarse habit with stout subligneous base nearer *P. robustius;* in foliage intermediate; in the spike showing the slender habit of *P. hydropiperoides* and the purple color of the rhachis, but in the large milk-white flowers and the great length of the spikes suggesting *P. robustius*. .Practically all the achenes are empty. Out of 135 sheets of specimens collected on August 29 we were able to secure only 5 partially filled achenes; while a mass of 100 or more older inflorescences collected in September by Mr. McPherson yielded no good achenes."

Both the parents of this plant are perennials, and, while seeding freely, also perennate by rhizomatiform stems. The hybrid colony, according to a personal statement to the writer by Professor Fernald, covered a space of many square rods, was spreading rapidly by stem-rooting, and might conceivably have arisen from a single seed.

Preliminary examination of the considerable amount of material ascribed by its various collectors to *Polygonum hydropiperoides* Michx., *P. amphibium* L., [*P. natans* (Michx.) Eaton] and *P. Muhlenbergii* Wats. [*P. coccineum* Muhl.] and accumulated in the Gray Herbarium indicated that here were three essentially well defined species whose representatives, while agreeing sufficiently with the normal type to be generally referred there, yet differed habitally and technically in a highly erratic manner. The material of *P. hydropiperoides*, a species more closely related to the bulk of the subgenus than the other two, often suggested a blending with other species. That of the amphibious species, which were apparently closely related, but not particularly akin to any other well recognized species in North America, often approached each other quite closely, particularly in aquatic phases. The opportunity of comparing conditions existing in this material with the better defined species of the group and that of the characteristic and well-defined hybrid above cited suggested that the latter might serve as well as an artificially produced hybrid for the establish-

ment of some idea as to whether the variations in these puzzling species might be due to the variability common in semi-aquatics, whether they represented more stable developments worthy to rank as varieties or possibly species, or whether the possibility of hybridism might also enter in.

The consideration of hybridism, naturally, was correlated with the study of flower-forms referred to more particularly in another paper,[1] in order to determine by what means such crossing might be brought about, as well as to consider the possibility of permanency of variations thus established. While the more showy species of *Persicaria* have well developed nectaries, and, to quote from a private communication from E. F. Phillips, Apiculturist, United States Department of Agriculture, "yield considerable quantities of nectar and are important honey plants,"[2] it is the writer's belief that close-fertilization is the rule and cross-fertilization the exception in the Persicarias of the northern and western states, with the exception of the amphibious group and possibly others of heterostyl habit in which the reverse is true. Granted a fertile close-fertilized hybrid, however, the chances of its survival would appear to be considerably greater than of one of a group in which cross-fertilization is the rule. Perennial Persicarias, of which *Polygonum natans*, *P. coccineum*, and *P. hydropiperoides* are evident examples, also occur in some number in America, in contrast to the condition in Europe, where *P. amphibium* is the only perennial. Their hybrids, like that cited above, would naturally tend to persist longer than those restricted to seed reproduction by annual habit.

In view of the recent interest in pollen conditions as a criterion of hybridism[3] the examination of the pollen of these plants at once

[1] Stanford, RHODORA, xxvii. 41–47 (1925).

[2] According to Pellett (Am. Honey Pl.), *P. Persicaria*, "heart's-ease," is the most generally important in this respect, though it varies greatly in value in different sections of the country. "This plant, so valuable in Illinois and Nebraska, is of no importance in Maine; a bee is rarely seen on the flowers." "The honey . . . varies greatly, both in quantity and quality. Some species do not seem to yield at all, at least not regularly, while others produce large quantities of nectar." This writer also counts the amphibious Persicarias as valuable honey-plants. Knuth (Handb. Fl. Poll.) from European studies, does not assign *P. Persicaria* or any other member of the genus especially high rank as a bee-plant. Jepson (Fl. Calif.) cites *P. acre* (*P. punctatum* Ell.) as an important honey-plant in California, although it seems not to be highly ranked elsewhere. Regional influence on honey-production seems much in need of study.

[3] The scope of the present paper does not permit a review of the extensive literature on pollen sterility, or a summary of the divergent opinion as to the value of defective pollen as a criterion of hybridism. Among the more recent American contributions

suggested itself. For this purpose the pollen of the staminate type of flower was used, as being much more abundant. For examination flowers on the verge of opening, but as yet unfolded, were chosen. After opening, both the pollen and the anthers soon disappear, and the flowers are often spoiled for the present purpose by the introduction of foreign pollen. The anthers were mounted in water, the pollen teased out and examined with various powers of the compound microscope. Water is not a proper mounting material for all types of pollen, but gives good results with that of *Persicaria* as obtained from dried herbarium material. Inasmuch as no germination tests could be carried out, no attempt was made to estimate exact percentages of imperfect pollen, although in most cases this could probably be done with a fair degree of accuracy. Variation between different specimens clearly referable to the same species is sufficient to render estimates based on examination of less than some scores of specimens more or less of an approximation.

The pollen of the subgenus *Persicaria* is spherical or nearly so, dark-pigmented, yellowish-brown under the microscope, and marked hexagonally more or less in relief. The diameter, in apparently average material, varies from 0.033–0.040 mm. in *Polygonum lapathifolium* to 0.060–0.066 mm. in *P. coccineum* (0.092 mm. in the more abnormal of the latter species). That of *P. hydropiperoides* averages 0.043–0.050 mm. in material showing virtually all apparently good pollen; this species is one of the more variable in the size, shape, and apparent quality of the anther-contents. The pollen of *P. robustius* is of approximately the same size; in this species it appears much more constantly normal, although the number of available specimens was not large.

In general it may be said that the report of Schuster that frequent variations exist in apparently good species was confirmed. The amount of variation differs widely in different species, and in different material, apparently typical, of the same species. In *Polygonum pensylvanicum*, for instance, as well as in *P. robustius*, the grains are usually very constant in size and only occasional plants show a variable proportion (10% or more) of defective individuals. That of

---

to the subject mention might be made of the study of blackberries by Brainerd and Pieterson, in which, as pointed out by Fernald (RHODORA, xxii. 185–191) a number of well recognized species are described as having from 70% to 85% of imperfect pollen, while others are listed as hybrids of such species, yet having as low as 10% imperfect pollen.

the essentially monotypic *P. virginianum* L. (subgenus *Tovara*) is extremely constant.

The flowers of *Polygonum hydropiperoides* × *robustius* are of the open type, while the panicles of its parents usually contain both types. The pollen of the hybrid is produced in considerable quantity, though less abundantly than in the open flowers of the parent species, and is very variable in size and appearance. The grains range from 0.016–0.066 mm., the smaller evidently empty or distorted and nearly or quite unpigmented. Judging from the microscopic appearance in comparison with apparently normal pollen of other species, not over 5–10%, probably much less, could function. Correlated with this is a complete lack of development of the ovary, from which coordinate conditions in the egg may be deduced. A very similar type of defective pollen occurs frequently in specimens referred to *P. hydropiperoides*. Occasionally it is accompanied by wide-open evidently infertile flowers, in plants whose considerable variance from the type is often suggestive of mixed parentage with a more or less definite indication of the other species involved. More commonly it accompanies an apparently normal achene-production. Sometimes plants with apparently normal achenes and a large proportion of defective pollen appear inseparable from the type; more frequently, however, points of variance may be found. In this species the problem is complicated by the appearance of occasional plants apparently wholly of the pistillate type, with little or no pollen, and occasionally (more rarely) plants of the staminate type. It may be said that the appearance of considerable percentages of defective pollen in *P. hydropiperoides* is usually, but not invariably, connected with an "off-type." In the closely related *P. opelousanum* Riddell a variation was found which appears to be a blend of that plant with *P. punctatum* Ell. Specimens in most cases showed defective pollen, but the plant produced achenes in profusion.

Foreign hybrid material in the Gray Herbarium is exemplified by specimens referred to *Polygonum lapathifolium* × *Persicaria*, *P. Hydropiper* × *minus*, *P. Hydropiper* × *mite*, *P. minus* × *Persicaria*, and *P. mite* × *Persicaria*. In general these specimens reveal a median character between their supposed parents and show pollen- and achene-characters comparable with some of the "off-types" discussed above.

In *Polygonum natans* and *P. coccineum* the segregation of flower-types somewhat complicates matters. In the long-styled flowers

pollen is usually absent. The ranges of the two species largely coincide except for a central area running southward and southwestward from Illinois, where *P. coccineum* runs southward into Mexico, apparently unaccompanied by *P. natans*. Where the ranges coincide the pollen of the short-styled flowers usually shows a large percentage of defective grains of a type quite comparable with that of the Nova Scotian hybrid above referred to. The long-styled panicles usually show a high degree of infertility and are often entirely barren. In the central belt mentioned, the pollen of the short-styled flowers of *P. coccineum* is usually normal, and the fertility of the other type appears to run higher, though still below what would be considered normal in another species.

Examination of all the short-styled specimens of *P. amphibium* L. in the Gray Herbarium (12 sheets) showed only one where the pollen was noticeably abnormal. In this European species, as in *P. coccineum* in the central North American belt referred to, the fertility of long-styled panicles is below what would be expected in another species, especially in the terrestrial form. Rather surprisingly, in the American *P. natans*, forma *Hartwrightii*[1] the pollen seems to be more nearly normal than in the aquatic form, although the latter is more frequently productive of achenes.

It appears probable that the cause of sterility in these perennials is in part bound up with the development of a vegetative mode of perennation and spreading, and not unlikely that in the American species the condition is further complicated by a considerable amount of cross-breeding; the result of these two factors, together with the variability common to aquatics, being visible in the highly variable series of plants so liberally christened by Greene.[2]

As a general conclusion it may be stated, that the evidence does not warrant changing the systematic rank of species or varieties which are known to be self-perpetuating and which have become more or less widespread over a definite range, but it does, in the present state of our knowledge, indicate the advisability of caution in the proposal of new species or varieties on the basis of variations seen in occasional herbarium sheets which show a considerable proportion of defective pollen and about the range and fertility of which little or nothing is known.

Western Reserve University.

[1] Polygonum natans, forma **Hartwrightii** (Gray), comb. nov. *P. Hartwrightii* Gray, Proc. Am. Acad. viii. 294 (1870). To be discussed in succeeding paper.

[2] Greene, *Certain Polygonaceous Genera.* Leafl. i. 17–50 (1904).